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EGG AND LARVAL DEVELOPMENT OF SPANISH SARDINE, *SARDINELLA AURITA* (FAMILY CLUPEIDAE), WITH A SYNOPSIS OF CHARACTERS TO IDENTIFY CLUPEID LARVAE FROM THE NORTHERN GULF OF MEXICO

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ABSTRACT

Larvae of the Spanish sardine are poorly known and the taxonomy of *Sardinella* species are poorly understood. Despite high morphological variability in adults, recent evidence provides no clear indication of two sympatric species of *Sardinella* in the western Atlantic Ocean and all are considered *S. aurita.* Larval evidence supports the high morphological variability reported for adult Spanish sardine, but does little to augment the understanding of *Sardinella* taxonomy in the western Atlantic. Eggs and larvae of *S. aurita* are described in this paper. Spawning apparently occurs at night. Eggs average 1.08 mm in diameter, have a single oil globule, and are smaller than those of most other clupeids. Length-at-hatch is about 2.5 mm standard length and growth in the laboratory averaged about 0.8 mm·day^{-1} at 26–27°C. Transformation begins at 16 mm and is complete at 23 mm. During transformation, full complements of fin rays develop, the gut shortens, and dorsal and anal fins move forward. Larval development of Spanish sardine off Brazil is delayed compared to that of northern Gulf of Mexico specimens. Larvae of *S. aurita* are recognized primarily by melanophores bilaterally situated on the nape. Pigment differences provide a more versatile taxonomic character than myomere counts alone for identifying clupeid larvae because myomere counts overlap among some species. Primary pigmentation characteristics that separate larval clupeids, including *S. aurita,* from the northern Gulf of Mexico are: 1) presence or absence of pigment at the notochord tip and on the nape; and, 2) the standard length at which pigment appears along the cleithrum both above and below the pectoral fin, dorsally along the hindgut, and along the caudal peduncle.

Taxonomy of *Sardinella* species in the western Atlantic Ocean is poorly understood. Regan (1917) recognized a single western Atlantic species (*S. aurita* Valenciennes). Hildebrand (1963), however, referred to his western Atlantic material as *S. anchovia* Valenciennes and recognized a second species with a higher gillraker count, *S. brasiliensis* (Steindachner), that ranged from south Florida to Brazil. Prosvirov and Varea (1969) believed that only one species (*S. anchovia*) occurred in the Gulf of Mexico (Gulf). Whitehead (1973, 1985) synonymized *S. anchovia* with *S. aurita* and recognized *S. brasiliensis* as a sympatric species. Roithmayr (unpublished data)[1] agreed with Whitehead (1973, 1985) and concluded that both species occur in the Gulf, with *S. aurita* more abundant than *S. brasiliensis.* Both Roithmayr and Whitehead also agreed that overlap in gillraker counts at <130 mm SL confounds any clear-cut distinction between taxa, a situation further complicated by the potential influence of exogenous factors on meristics (Whitehead, 1973). Despite high morphological variability in *Sardinella,* a recent electrophoretic study of Spanish sardine from the Gulf of Mexico and off Brazil found no clear indication of two sympatric species (Wilson and Alberdi, 1991).

Sardinella aurita occur in both the eastern and western Atlantic Oceans, including the Mediterranean Sea, where its breeding patterns are extremely complex (Whitehead, 1985). Numerous populations or races of the species are believed to

[1] National Marine Fisheries Service, Southeast Fisheries Center, Pascagoula, Mississippi.

exist, further complicating the understanding of its systematics, reproductive biology, and early life ecology.

Current literature on *Sardinella* larval development is inadequate to reliably separate Spanish sardine from other clupeids in the Gulf. Eggs and yolk-sac larvae of *S. brasiliensis* have been illustrated (Matsuura, 1971), but most descriptions of larvae are based on specimens from areas outside the Gulf and many illustrations are of low quality (Fage, 1920; Whitehouse, 1933; d'Ancona, 1956; Conand and Fagetti, 1971; Matsuura, 1975). Larval *Sardinella* <20 mm in length from southern Brazil cannot be separated into two groups using gillraker counts or other characters and no distinct pigmentation pattern has been found to distinguish larvae of *Sardinella* from that region from larvae of other clupeids (Matsuura, 1975). Other authors have discussed characters useful for separating larvae of Gulf clupeids (Houde and Fore, 1973; Houde et al., 1974; Houde and Swanson, 1975; Hettler, 1984), but these descriptions rely primarily on myomere counts and presence/absence of pigment above the notochord tip, and do not adequately address *Sardinella* identification. Our objectives are to describe the egg and larval development of Spanish sardine from the Gulf, to compare the developmental morphology of *Sardinella* from the Gulf and Brazil, and to provide additional characters for separating *Sardinella* larvae from those of other Gulf clupeids.

Materials and Methods

Wild-caught *Sardinella* larvae were obtained from obliquely-towed 60-cm bongo net (0.333 mm mesh) and surface-towed 1 × 2 m neuston net collections taken throughout the Gulf in conjunction with Southeast Area Monitoring and Assessment Program (SEAMAP) surveys.[2] Collection methods are detailed in Kelley et al. (1986). Eggs were collected in the Gulf Stream off Miami, Florida, with a 1-m diameter plankton net on 5 and 10 September 1969, and brought to the laboratory for culture experiments. Surface water temperatures were 29°C at collection. Rearing techniques were similar to those described by Houde and Palko (1970) and Houde (1973). Temperatures and salinities during rearing were 24.2–27.5°C (usually 26.0–26.5°C) and 32.4–34.4‰. Larval growth data are from laboratory-reared specimens.

We examined 29 wild-caught and three lab-reared Spanish sardine larvae between 3.7 and 36.8 mm to describe pigmentation and larval development (Table 1). Information on early larval pigmentation and developmental morphology was primarily from wild-caught larvae but was supplemented with data from laboratory-reared specimens. We also examined wild-caught larvae from waters off southern Brazil for comparison. Body measurements were to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope. We considered notochord length in preflexion and flexion larvae synonymous with standard length (SL) in postflexion larvae and all lengths are SL unless otherwise noted. Body measurements follow Hubbs and Lagler (1958); myomere counting procedures were slightly modified from those of Hettler (1984). Definitions and other terminology are as follows:

Epimeres—segment of muscle lying dorsal to mid-lateral septum.

Hypomere—segment of muscle lying ventral to mid-lateral septum.

Total myomeres—all myomeres between the most anterior and posterior myosepta. This excludes both the triangular area preceeding the first myoseptum and the urostylar segment.

Preanal myomeres—number anterior to and including the myomere in contact with the downward curve of the anus in larvae without anal fin rays.

Postanal myomeres—number posterior to the anus and non-overlapping. This count includes the myomere in which the anteriormost anal fin ray is inserted. Once anal fin pterygiophores develop, the first anal fin ray often was inserted into the myomere overlapping the anus.

Predorsal myomeres—number anterior to and excluding the myomere in contact with the anteriormost dorsal fin ray.

Postdorsal-preanal myomeres—number posterior to and excluding the myomere in contact with the posteriormost dorsal fin ray and either overlapping the anus in larvae without fin rays, or anterior to the myomere in contact with the anteriormost anal fin ray.

Anterior- and posterior-most myomeres were difficult to count on larvae <6 mm and >17–18 mm.

[2] SEAMAP, 1982–1986 Gulf of Mexico Biological Data Set. National Marine Fisheries Service, Southeast Fisheries Center, Ocean Springs, Mississippi: Gulf States Marine Fisheries Commission.

Table 1. Body measurements (expressed as % standard length [SL]) of Spanish sardine (*Sardinella aurita*) larvae from the Gulf of Meixco. All larvae are wild-caught except those between 19.3 and 36.8 mm SL which are laboratory-reared. Proportions were rounded to the nearest 0.5%. Dashes indicate no fin base development; asterisks indicate no measurement.

SL	N	Preanal length	Head length	Snout length	Eye diameter	Body depth pectoral	Predorsal length	Prepelvic length
3.0–3.9	3	84.5–85.0	14.0–19.0	2.5	6.5–7.0	10.5–11.0	—	—
4.0–4.9	2	83.5–84.5	14.5–15.5	2.0	5.0–5.5	8.5–10.0	—	—
5.0–5.9	1	88.0	16.0	3.5	5.0	8.5	—	—
6.0–6.9	2	86.5–87.5	16.5–21.0	3.5–5.0	5.0–6.5	8.5–10.0	68.5	—
7.0–7.9	3	87.0–89.0	20.5–22.0	3.0–5.5	4.5–6.5	9.0–11.0	65.0–69.0	—
8.0–8.9	2	86.0–88.0	20.0	4.5–5.0	5.0–5.5	10.0–10.5	64.5–65.5	—
9.0–9.9	3	87.0–89.0	17.5–20.5	4.0–5.5	5.5–6.0	8.5–9.5	65.0–66.5	—
10.0–10.9	2	86.0–88.5	21.0–22.5	5.0–6.5	5.5–6.0	10.0–10.5	65.0–66.5	50.5
11.0–11.9	1	85.5	22.0	5.5	6.0	10.0	64.0	49.5
12.0–12.9	2	85.0	21.0–23.5	5.5–6.5	5.0–6.5	10.5	64.0–69.0	48.5–52.5
13.0–13.9	3	83.5–86.5	21.0–22.0	5.5	5.5–6.0	10.5–11.0	62.0–63.5	47.0–47.5
14.0–14.9	1	85.0	22.0	5.5	5.5	10.5	61.5	49.5
16.0–16.9	2	80.0–81.0	23.5–24.5	6.0	6.0–6.5	12.0–12.5	57.0–58.0	47.5–49.5
18.0–18.9	2	78.0–79.0	26.5–27.0	6.5–7.0	7.0–7.5	14.5–15.0	52.5	48.5–51.5
19.3	1	78.0	25.0	6.5	6.5	18.0	49.0	*
23.1	1	76.5	27.0	7.5	6.5	19.5	43.5	*
36.8	1	73.5	29.0	8.0	6.5	24.5	41.5	*

Myomere #2 was usually the first complete myomere. Myomeres changed shape and became splayed as larvae increased in length. For consistency with our counting procedures, location of dorsal and anal fins with respect to the body were determined by the position of the first dorsal and anal pterygiophores in relation to the ascending arm of the epimere or descending arm of the hypomere. Fin rays were counted on unstained larvae when pterygiophores were visible. Transforming larvae were those with rapidly-changing morphometrics and a full complement of rays in all but the pectoral fin. Pectoral rays do not form in clupeiform fishes until late in the larval period or during transformation (Moser and Ahlstrom, 1970). Transformation was complete when a full complement of rays was present in all fins and specimens had scales. We accepted the Wilson and Alberdi (1991) taxonomic analysis and considered all *Sardinella* larvae to be *S. aurita.* Representative specimens were illustrated by camera lucida.

RESULTS

Description of Embryos.—Six fertilized eggs from plankton collections 1.03–1.12 mm in diameter ($\bar{x}$= 1.08 mm); yolk diameters 0.54–0.62 mm ($\bar{x}$= 0.59 mm); oil globule diameters 0.13–0.18 mm ($\bar{x}$= 0.16 mm). Eggs spherical and similar to those from Venezuela (Simpson and Gonzalez, 1967) and Brazil (Matsuura, 1971). Embryos well-developed when preserved; eye, heart, and myomeres visible; tail free from yolk. Embryos with one oil globule in posterior-third of yolk-sac near ventral margin of yolk. Segmentation of yolk inconspicuous in preserved specimens but clearly visible in living embryos. Chorion thin, unpigmented, and unsculptured. Preserved embryos unpigmented, living embryos with very fine melanophores dorsally on anterior-half of body. Perivitelline space relatively wide, resembling that of most clupeids (except *Brevoortia* spp., menhaden; and *Etrumeus teres,* round herring). Spawning probably at night because all embryos well-developed when collected during day. Larvae hatched by early afternoon in laboratory. Predicted total incubation time of 24 h at 29°C (surface water temperature during collection), based on our mean egg diameter of 1.08 mm and Pauly and Pullin's (1988) relationship between egg diameter and water temperature which predicts development time to hatching in marine fishes.

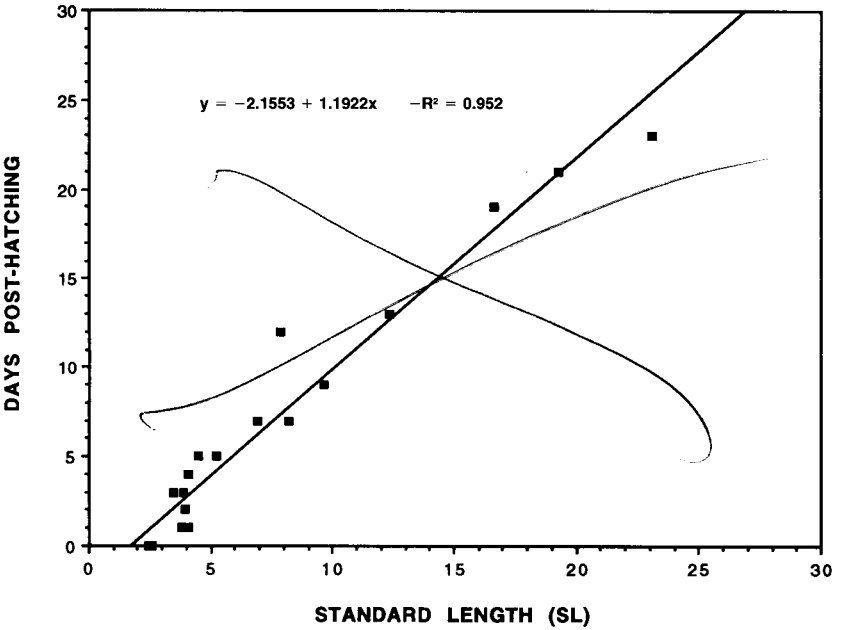

Figure 1. Growth of laboratory-reared Spanish sardine (*Sardinella aurita*) at 26–27°C.

Growth and Developmental Morphology.—Laboratory-reared Spanish sardine larvae hatched at 2.5 mm. No increase in length between days 1 and 4 post-hatching for most lab-reared larvae. Growth thereafter about 0.8 mm·day^{-1} (at 26–27°C) until day 23 (Fig. 1). Only one laboratory-reared specimen survived beyond 23 days and was 36.8 mm SL (44 mm total length [TL]) at day 40.

Recently-hatched, laboratory-reared larvae elongate, body depth usually 10% SL. Eyes round, body unpigmented. Yolk-sac elliptical; oil globule in posterior-third near ventral margin. Yolk vaguely segmented. Body with about 45 myomeres, posteriormost difficult to count. One-day-old larva (3.9 mm) with thin, straight gut, eyes becoming pigmented, much of yolk absorbed. Mouth and pectoral fins developing; 38 preanal and 8 postanal myomeres. By day 2, eyes fully-pigmented, pectorals well-developed. Larvae actively feeding by day 3. By day 5 (4.5–5.0 mm), fore- and hind-gut differentiated, hindgut with bands of muscle; liver below anterior portion of foregut. By day 7 (8.2 mm), swim bladder (located above junction of fore- and hind-guts) forming; inflated by 12.0 mm.

Morphometrics changed relatively little prior to transformation. During notochord flexion (6.0–9.5 mm, usually >7.5 mm), most body measurements greater relative to SL because body shorter due to upturning notochord. As larvae grew, SL decreased slightly relative to TL because of caudal fin ray development. Preanal length usually >85% SL in flexion and postflexion larvae <15 mm; thereafter, preanal length gradually decreased to 73.5% SL by 36.8 mm. Transformation to juvenile stage began at about 16.0 mm. During transformation, head length, snout length, and body depth increased proportionally relative to SL, whereas predorsal and preanal lengths decreased. Prepelvic distance and eye diameter proportions relatively stable with growth (Table 1).

ERRATA

Ditty, J. G., E. D. Houde, and R. F. Shaw. 1994. Egg and larval development of Spanish sardine, Sardinella aurita (Family Clupeidae), with a synopsis of characters to identify clupeid larvae from the northern Gulf of Mexico. Bull. Mar. Sci. 54(2): 367-380.

Change in Abstract on page 367, line 9, should read "Length-at-hatch is about 2.5 mm standard length and growth in the laboratory averaged about 0.8 mm/day^{-1} at 26-27°C."

Change in Results on page 370, line 3, should read "Growth thereafter about 0.8 mm/day^{-1} (at 26-27°C) until day 23 (Fig. 1)."

Figure 1, page 370. The independent and dependent variables are reversed. Standard length should be plotted on days post-hatching. The correct growth rate as derived from the growth equation is 0.84 mm/day^{-1} at 26-27°C. Figure 1 should be replaced as follows:

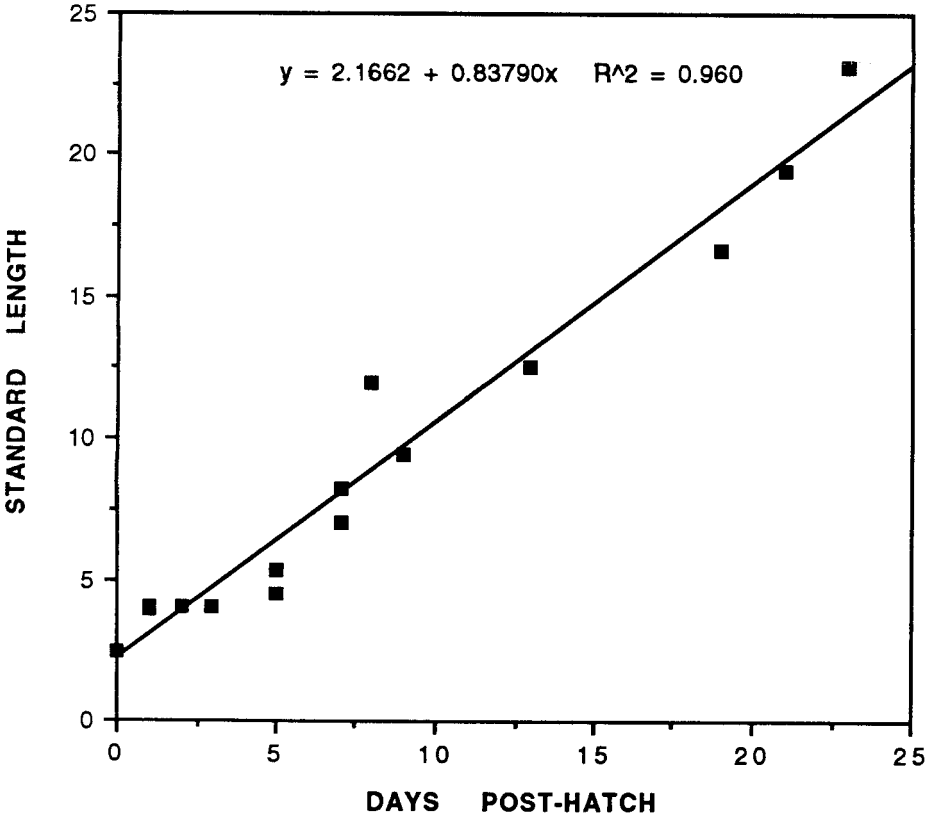

Fig. 1 Growth of laboratory-reared Spanish sardine (*Sardinella aurita*) at 26-27°C.

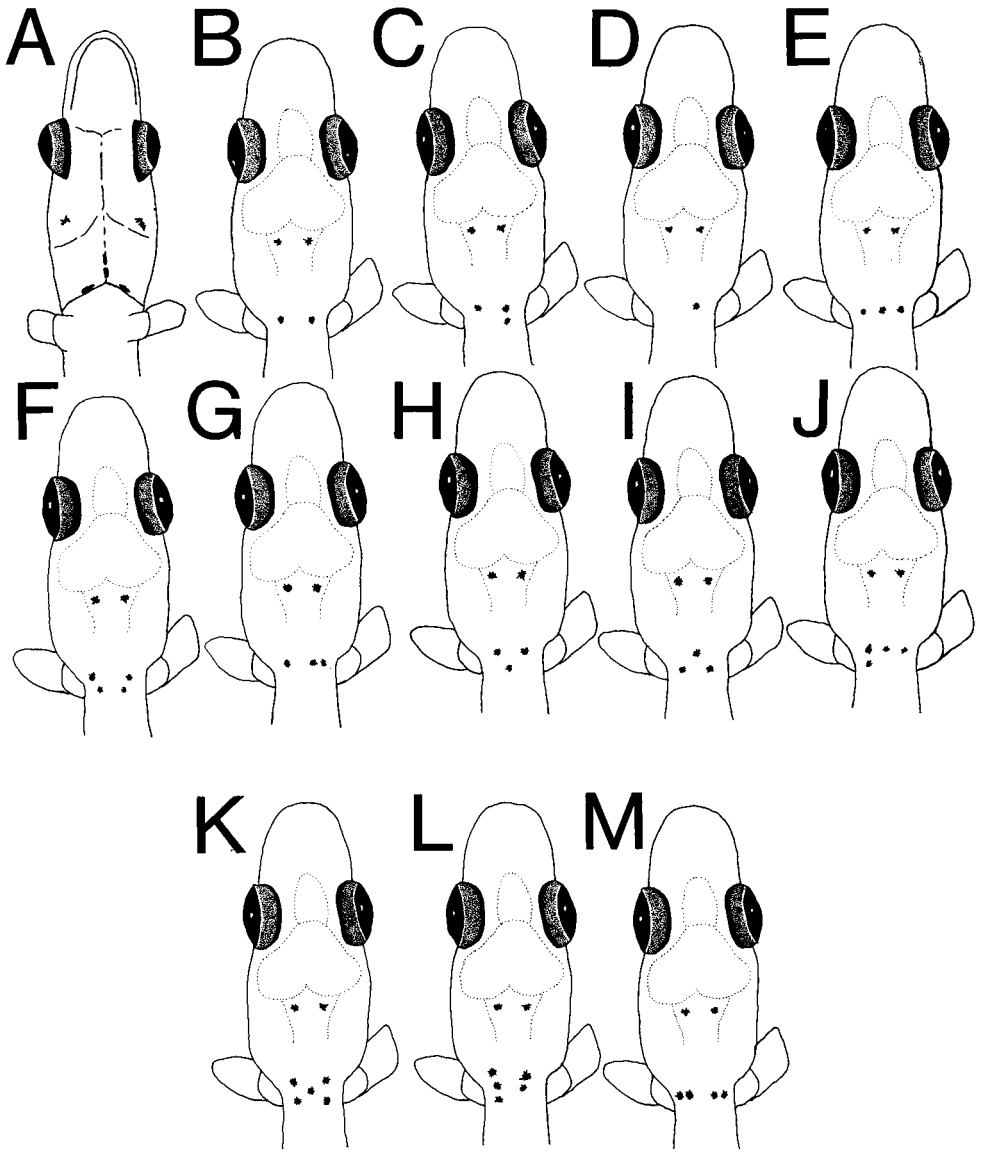

Figure 2. Diagrammatic illustration of pigment patterns ventrally along the cleithrum (A), and on the nape (B–M) of Spanish sardine larvae (*Sardinella aurita*) from the northern Gulf of Mexico. Nape patterns B through F occurred on 92% of Spanish sardine larvae.

Pigmentation.—Head pigment primarily concentrated on nape, along cleithra, and above junction of mid- and hind-brain prior to transformation (Fig. 3). Pigment usually on nape at all sizes but number and position of these melanophores varied. Twelve different nape pigmentation patterns identified on larvae between 4 and 10 mm (N = 100) (Fig. 2). Typically, one small, external melanophore bilaterally on each side of nape (64% of larvae), but 8% with single melanophore unilaterally. Other variations: 1) two melanophores laterally along one side of nape mid-

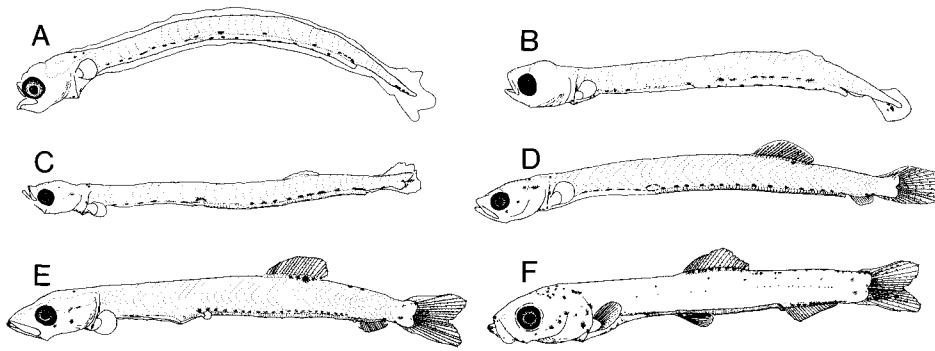

Figure 3. Larval development of Spanish sardine (*Sardinella aurita*) from the northern Gulf of Mexico. A. 3.6 mm, B. 5.5 mm, C. 8.1 mm, D. 11.8 mm, E. 14.0 mm, F. 19.0 mm. All measurements are mm standard length (SL).

line and single melanophore on opposing side (10%); 2) two melanophores bilaterally along each side of nape (5%); or, 3) melanophore in nape midline, which in conjunction with bilateral melanophores formed transverse row across nape (5%). Triangle of pigment when median melanophore either anterior to or posterior to bilateral melanophores (2%) (Fig. 2). Nape melanophores obscured by overlying musculature by 13.0–13.5 mm. Pair of melanophores externally near junction of mid- and hind-brain (Fig. 2) and single melanophore internally in otic region by 6.0–6.5 mm (Fig. 3). Two pairs of melanophores externally above junction of mid- and hind-brain by 13.0–13.5 mm. External melanophore on cheek by 10.0–10.5 mm; melanophore below eye and another ventrally near tip of lower jaw by 11.5–12.0 mm (Fig. 3). External melanophore ventrally along posterior portion of dentary immediately anterior to quadrate bone by 14.0 mm; pigment at premaxillary symphysis by 16.5 mm (Fig. 3). Along cleithrum, usually one melanophore dorsal to pectoral axilla by 4.0 mm, often hidden by axilla in small larvae. By 5.0 mm, elongate melanophore along cleithrum below pectoral axilla (Fig. 3). By 7.0 mm, pigment along isthmus and that along cleithra below pectoral axilla (when viewed ventrally) formed inverted "Y" (Fig. 2A). This "Y" less obvious as larvae grew. Head pigmentation increased during transformation (Fig. 3).

Abdominal pigmentation of Spanish sardine larvae relatively sparse with pigment primarily along gut (Fig. 3). In preflexion larvae <4.0 mm, row of elongate external melanophores above foregut of wild-caught larvae. No pigment ventrally

Table 2. Summary of fin development in Spanish sardine (*Sardinella aurita*) larvae as a function of standard length (SL). Adult ray complements are from Hildebrand (1963) and Whitehead (1973).

	mm SL			
Fin	Fin bases	First pterygiophores appear	Full ray complement present	Adult ray complement
Principal caudal	5	7.5	13–14	19
Dorsal	6	9.5	16–17	16–19
Anal	8	9.5	16–17	16–20
Pelvic	11	12.5	18	7–8
Pectoral	<4	16.0	23*	15–16

* Laboratory-reared specimen.

Table 3. Summary of comparative clupeid egg, yolk, and oil globule diameters (mean over range) from studies throughout the western Atlantic (P = plankton, A = artificially fertilized, B = both; dashes mean data not available)

Taxa	Author	Diameter (mm)			Study
		Egg	Yolk	Oil globule	
Brevoortia patronus	Houde and Fore, 1973	1.16* (1.04–1.30)	— —	— (0.08–0.20)	P
	Hettler, 1984	— (1.18–1.22)	— (0.66–0.79)	— (0.16)	A
B. smithi	Reintjes, 1962	1.34 (1.21–1.48)	0.90 (0.77–1.04)	0.13 (0.05–0.18)	P
	Reintjes, 1962	1.22 (1.15–1.30)	0.86 (0.77–0.95)	0.13 (0.07–0.16)	A
	Houde and Fore, 1973	1.34 (1.21–1.48)	— —	— (0.05–0.18)	P
	Houde and Swanson, 1975	1.27 (1.21–1.34)	1.07 (0.80–1.19)	0.15 (0.12–0.17)	P
B. tyrannus	Kuntz and Radcliffe, 1917	— (1.40–1.60)	— 0.90	— (0.12–0.14)	P
	Hettler, 1984	— (1.54–1.64)	— (0.82–0.95)	— (0.20–0.23)	A
Etrumeus teres	Houde and Fore, 1973	1.29 (1.17–1.37)	— —	— ABSENT	P
Harengula jaguana	Matsuura, 1972	1.64 (1.48–1.72)	— —	0.09 (0.07–0.10)	A
	Houde and Fore, 1973	1.66 (1.55–1.85)	— —	0.09 (0.07–0.10)	P
	Houde et al., 1974	1.66 (1.55–1.78)	— (0.63–0.72)	0.09 (0.07–0.10)	P
	Gorbunova and Zvyagina, 1975	— (1.35–1.98)	— (0.80–0.85)	— (0.07–0.10)	A
Opisthonema oglinum	Houde and Fore, 1973	1.19 (1.08–1.31)	— —	— (0.12–0.16)	P
	Richards et al., 1974	1.19 (1.10–1.28)	0.63 —	0.15 (0.12–0.16)	P
Sardinella spp.	Matsuura, 1971	1.18 (1.00–1.32)	— —	0.14 (0.09–0.18)	B
	Houde and Fore, 1973	1.12 (1.03–1.25)	— —	— (0.13–0.18)	P
	This study	1.08 (1.03–1.12)	0.59 (0.54–0.62)	0.16 (0.13–0.18)	P

* Mean over (range).

along foregut except immediately anterior and posterior to cleithral symphysis (Fig. 3). Usually three to five melanophores dorsally along hindgut either externally or in body musculature and one to three near anus. Parallel row of elongate melanophores ventrally along hindgut, these rows becoming staggered as larvae grew. Number of melanophores dorsal to hindgut increasing with SL; these melanophores partially obscured by overlying musculature by 13.0–13.5 mm. Usually one to two melanophores along ventral midline of caudal peduncle by 7.5–8.0 mm, these melanophores near anal fin termination and posterior to fin base (Fig. 3). External melanophore near posterior-third of dorsal fin base by 11.5–12.0 mm; one to two melanophores along dorsal midline of caudal peduncle by 13.0–13.5 mm (Fig. 3). Laterally, no external pigment on Spanish sardine larvae until 16.0 mm, when melanophores along lateral midline between dorsal fin termination and anal fin origin (Fig. 3). Internally, unevenly spaced row of mela-

Table 4. Myomere counts for clupeid larvae from the northern Gulf of Mexico. N = 2 for each size category. Acronyms are as follows: BP = *Brevoortia patronus,* ET = *Etrumeus teres,* HJ = *Harengula jaguana,* OG = *Opisthonema oglinum,* and SA = *Sardinella aurita.* Dashes indicate either no fin base development or no count.

Length (mm SL)	Preanal					Postanal					Predorsal
	BP	ET	HJ	OG	SA	BP	ET	HJ	OG	SA	BP
4.1–6.0	36–37*	—	34–36†	41	38–40	8*	—	5–7†	3–4	6–7	—
6.1–8.0	36–37*	39	35	40–41	38	7–9*	8–9	5–6	3–4	7	28–30*
8.1–10.0	35–38*	38–39	33–34	39–40	38–40	8–10*	8–9	6	4–5	6–7	26–28*
10.1–12.0	33–37*	37–39	32–34	38–39	37	8–10*	8–10	7–8	6	7–8	23–27*
12.1–14.0	33–35*	38–40	33	37–38	35	8–10*	8–9	7	6	8	23–25*
14.1–16.0	32–33*	37	31	37	36	9–10	10	8–9	6–7	8	22–23*
16.1–18.0	33	36–37	31	36–37	34–36	10–11	10	8	6–8	8–9	23
18.1–20.0	32	36–37	29–31	36	34	11	9–10	8–10	8	10	21–22
20.1–22.0	31	36	30–31	34–36	—	12	10	9	8–9	—	21

* From Hettler (1984); total myomere counts are mean values rounded to nearest whole number.
† From Houde et al. (1974).

nophores above anteriormost precaudal vertebrae and one to two melanophores above last few caudal vertebrae by 12.0–13.0 mm. Additional pigment internally above vertebrae and externally along abdomen as larvae grew.

Caudal pigment primarily ventral to notochord tip in preflexion and flexion larvae (Fig. 3) and rarely (only once) above tip. During notochord flexion, pigment externally at junction of dorsal and ventral hypurals and proximally on developing caudal fin ray anlagen. By 12.0 mm, melanophore externally above urostyle near base of uroneural and internally ventral to urostyle. Pigmentation increasing over caudal fin as larvae grew (Fig. 3).

Fin Development.—Dorsal and anal fin bases originated as thickened ridges along their midlines at about 6.0–6.5 and 7.0–7.5 mm, respectively. Differentiation of both fin bases in posterior to anterior direction. Full complement of dorsal and anal rays by 16.0–17.0 mm. Pelvic fin buds at 11.0 mm, with full complement of 7–8 rays at 18.0 mm. Neither scales nor full complement of pectoral rays in our largest wild-caught larva (18.5 mm); both characters in 23.1 mm lab-reared specimen (Table 2). Caudally, ventral thickening near tip of unflexed notochord by 5.0 mm. During flexion, anlagen differentiating obliquely downward in caudal finfold. Development of primary caudal rays outward from body midline, with ventral ray development slightly preceeding that of dorsal rays. Full complement of 19 primary caudal rays by 13.0–14.0 mm.

Discussion

Comparative egg, yolk, and oil globule diameters suggest that *Sardinella* eggs can be separated by mean egg size from most other northern Gulf clupeids (except Atlantic thread herring, *Opisthonema oglinum,* and gulf menhaden, *B. patronus*); mean egg diameter in Spanish sardine is smaller than most other clupeids although the range of egg sizes may overlap (Table 3). In addition, eggs of round herring (*E. teres*) lack an oil globule (Table 3). Scaled sardine (*Harengula jaguana*) eggs are larger (egg diameter usually >1.5 mm versus <1.4 mm in other species) and oil globule diameters smaller than in all other clupeids but menhadens, *Brevoortia* spp. Based on the seasonal occurrence of small clupeid larvae in the Gulf of Mexico north of 26°00′N (Ditty et al., 1988), however, *Brevoortia* eggs (October–March, peak December–February) would probably not occur with those of *H. jaguana, O. oglinum,* or *S. aurita* (March–October, peak spring–summer). *Bre-*

Table 4. Extended

Predorsal				Postdorsal–preanal					Total				
ET	HJ	OG	SA	BP	ET	HJ	OG	SA	BP	ET	HJ	OG	SA
—	—	—	—	—	—	—	—	—	44–45	47–48	40–41	44–45	45–46
—	24–26	26–27	27	4–6*	—	6–7	10	7–8	44–45	47–48	40–41	44	45
27–32	22–23	26–27	26–27	3–5*	4	6–7	8–9	8	45	47	39–40	44	45–46
27–30	21–23	24	24	3–4*	4	4–5	7–9	5–6	44–45	47	40–41	44–45	44–45
29	20–21	24–25	22–23	2–3*	4	4–5	7–8	5	43–44	47–48	40	43–44	43
27–28	18	24–25	22–23	1–2*	3	4–5	6–7	5–6	43–44	47	39–40	43–44	44
26–27	18	23	19–20	2	3	4–5	6–7	5–6	43–44	46–47	39	43–44	43–44
26	14–16	22–23	18	2	2–3	5–6	5–6	5	43	46	39	44	44
26	14–15	22–23	—	0–1	2	5–6	6–7	—	43	46	39–40	43–44	—

voortia and *S. aurita* eggs, however, may co-occur during winter months off South Florida and in the southern Gulf.

Off Brazil, *Sardinella* larvae hatch in about 24 h at incubation temperatures of 23°C (Matsuura, 1971). The effect of temperature on egg incubation (Pauly and Pullin, 1988), however, predicts hatching should occur at 38 h at 23°C and 24 h at 29°C. Our data suggest that hatching may occur at considerably <24 h (at rearing water temperatures averaging 26°C) because all embryos were well-developed when collected during the day and because hatching began by early afternoon in the laboratory.

As Spanish sardine larvae grow, number of preanal and predorsal myomeres decrease and postanal myomeres increase. At lengths between 6.0 and 10.0 mm, this decrease in predorsal length and number of myomeres (Tables 1, 4) is due to measurements and counts being made on larvae with partially formed dorsal fin bases. During early transformation (about 16.0 mm—Conand and Fagetti, 1971; this study; about 19.0 mm—Matsuura, 1975), decreasing preanal and predorsal lengths result from the anterior migration of dorsal and anal fins and progressive shortening of the gut. Postdorsal-preanal myomere counts decrease from 8 in preflexion Spanish sardine larvae to about 5 during transformation (Table 4). Sequence of fin formation is C-D-A-P_2-P_1 (Matsuura, 1975; Table 2).

Development of Spanish sardine larvae from Brazil is delayed with respect to those from the Gulf. We found the liver developing by 5.0 mm in Gulf larvae but not until 7.0 mm in larvae from Brazil. In addition, the anal fin base and pelvic fin buds form around 8.0 and 11.0 mm, respectively, in Gulf larvae but not until 10.0 and 13.5 mm in specimens from Brazil. Furthermore, both preanal and predorsal myomere counts are usually 1–2 higher in wild-caught larvae from Brazil. This results in preanal and predorsal measurements 3–5% higher and is consistent with the cooler developmental temperatures and slower development of dorsal and anal fin bases in Brazilian *Sardinella.*

Pigment patterns for specimens we examined from Brazil were unreliable because pigments had degraded from long-term storage in formalin. However, single melanophores did occur bilaterally on the nape in all but one specimen (N = 17). Matsuura (1975) did not discuss nape pigment but later examined samples of larval *Sardinella* from Dakar (Africa), Florida, and Brazil, and found a pair of melanophores in the occipital region of larvae from all three locations. Larval *S. aurita* from the eastern Atlantic Ocean off West Africa also have pigment on the

nape, a character apparently lacking in its congener, *S. maderensis* (Conand, 1978). Position of the pylorus with respect to the last few prepyloric melanophores also separates *S. aurita* from *S. maderensis* when <12.0 mm (Conand, 1978).

Larval evidence supports the high morphological variability reported for adult Spanish sardine by numerous authors, but does little to augment the understanding of *Sardinella* taxonomy in the western Atlantic. For example, 92% of *S. aurita* larvae from the northern Gulf had nape pigment patterns resembling Figure 2B–F. Nape patterns C, D, G, and probably J and L can occur on either side of the dorsal midline. In addition, variation evident in myomere counts and morphometrics between specimens examined from Brazil and those from the Gulf could be attributed to differences in water temperatures between locations during early larval development or to clinal differences between populations.

Inconsistencies among studies of clupeid larvae in defining myomere counting procedures has led to ambiguity in interpreting these data. Standardization is particularly important in clupeid larvae because number of postdorsal-preanal myomeres is used as a diagnostic character for separating genera. Neither Matsuura (1975) nor Powles (1977) specify their counting procedures for Spanish sardine or dwarf herring (*Jenkinsia lamprotaenia*), respectively. Other authors include the urostyle in counts (i.e., Houde et al., 1974; Richards et al., 1974; Houde and Swanson, 1975), but Hettler (1984) did not. In addition, most clupeid studies define counting procedures as "number of myomeres anterior or posterior to a vertical line through either the fin origin or termination" but do not specify where they include myomeres overlapping the line. Only Hettler (1984) defines myomeres anterior to and not overlapping the first dorsal ray as predorsal and those posterior to and not overlapping the last dorsal ray as postdorsal. Myomeres in contact with the anus are included with preanal counts.

Number of myomeres usually differ slightly from counts of vertebrae reported in the literature for clupeid larvae because posteriormost myomeres are difficult to count (Tables 4, 5). In general, counting myomeres is time-consuming and difficult (Hettler, 1984; this study). In addition, overlapping myomere counts and body measurements among most clupeids limit their use in clearly separating taxa. Rather, the value of counts (Table 4) and measurements lies primarily in separating species complexes. For example, number of total myomeres separate *H. jaguana* and *J. lamprotaenia* larvae (<42) from *B. patronus, B. smithi* (yellowfin menhaden), *O. oglinum,* and *S. aurita* (43–46); *E. teres* have ≥46 (usually 47–48) myomeres. Finescale menhaden, *B. gunteri,* have 42–43 total myomeres based on number of vertebrae (Dahlberg, 1970), but larvae are undescribed. In addition, postdorsal-preanal counts separate *H. jaguana* from both *O. oglinum* and *S. aurita* but do not separate *O. oglinum* from *S. aurita* (Table 4). We also found that although larval *Brevoortia* spp. and *E. teres* usually have fewer postdorsal-preanal myomeres than other clupeids of similar length, these aforementioned two taxa are not readily separated from each other because of overlapping counts (Table 4). Hettler (1984) considered a postdorsal-preanal myomere count of two or three diagnostic for *Brevoortia* at lengths >14.0 mm. *Brevoortia* spp. and *E. teres,* however, probably would not be confused because of other morphological traits.

Larval *J. lamprotaenia* probably do not occur in the northern Gulf but can be separated from other clupeids by lack of postdorsal-preanal myomeres at <12 mm (i.e., dorsal fin termination and anal fin origin occurs in same myomere; Powles, 1977). Similarly, preanal length separates larvae of *Brevoortia* spp., *E. teres,* and *J. lamprotaenia* (<85% SL, usually 82–83%) from *H. jaguana, O. oglinum,* and *S. aurita* (>85% SL, usually 88–90%) prior to early transformation, but not in-

Table 5. Summary of meristic, morphometric, and pigmentation characters for separating clupeid larvae <15 mm standard length (SL) in the northern Gulf of Mexico. *Jenkinsia* data are from Powles (1977); *B. smithi* are from Houde and Swanson (1975). Abbreviations are as follows: VAR = variable, UNK = unknown, P_1 = pectoral fin base, Sp = spring, Su = summer, F = fall, W = winter. Meristics are most common counts.

Character	*Sardinella aurita*	*Brevoortia patronus*	*B. smithi*	*Etrumeus teres*	*Harengula jaguana*	*Jenkinsia lampro-taenia*	*Opistho-nema oglinum*
Adult meristics							
Total vertebrae[1]	45–47	44–46	45–47	48–50	39–42	38–42	45–46
Dorsal rays	16–19	21–23	19–21	18–21	17–19	11–13	21–22
Anal rays	16–20	18–22	20–21	11–12	17–18	13–14	21–25
Pectoral rays	15–16	13–15	14–16	10	14–16	12–14	15–17
Postdorsal/preanal myomere counts							
<10 mm SL	7–8	4–5	4–5	4	6–7	0	8–10
10–15 mm SL	5–6	2–4	2–4	3–4	4–5	7–8[2]	6–8
Preanal length (%)[3]	≥85	<85	<85	≤85	>85	<85	>85
Pigmentation							
Notochord tip[4]							
Dorsal	No	VAR	VAR	No	Yes	No	No
Ventral	Yes	Yes	Yes	Yes	Yes	No	Yes
Nape							
Medial	VAR	Yes[5]	Yes[5]	No	Yes	No	No[5]
Bilateral	Yes	No	No	No	No	Yes[6]	No
Cleithrum[7]							
Above P_1	>4	>13[8]	UNK[8]	No	>8[9]	No	>15
Below P_1	>5	No	No	>12	No	>5	>15
Caudal peduncle[7]							
Dorsal	>13	VAR > 9	UNK	No	No	VAR[10]	No
Ventral	>8	>5–6	>4–5	>6	>11	>12	>12
Dorsal to hindgut	Yes	Yes	Yes	Yes[11]	Yes	Yes	No[12]
Spawning	Sp, S, F	F, W	F, W	W, Sp	Sp, Su	—	Sp, Su
Transformation[7]							
Initiation	16	19	14	17–18	14–15	12–15	15
Completion	23	25	20–23	30–33 TL	21–22	21	24
Other				HG > FG[13] LJ > UJ[14]			

[1] Myomere count should approximate total number of vertebrae. [2] No postdorsal-preanal myomeres at <12 mm, 7–8 by about 15 mm. [3] Proportions are %SL and prior to transformation at about 15 mm. [4] Preflexion larvae only. [5] Internal only above anterior precaudal vertebrae at >14 mm in *B. patronus*, >10 mm in lab-reared *B. smithi*, and at >15 mm in *O. oglinum*. [6] External bilateral at >9.4 mm; internal at >15 mm. [7] Measurements are in mm SL. [8] Along base of pectoral fin at >11 mm in *B. patronus* and >7 mm in *B. smithi*. [9] Also along pectoral fin base by 7 mm. [10] 50% of larvae have pigment between 5 and 12 mm. [11] Unpigmented gap along anterior hindgut. [12] At <9 mm. [13] Hindgut (HG) thicker than foregut (FG). [14] Length of lower jaw (LJ) > upper jaw (UJ).

dividual species within each group. Hettler (1984) discusses separation of individual species of *Brevoortia*.

Pigment differences constitute a more versatile taxonomic character than meristics because pigmentation can be used over a greater range in larval size (Moser and Ahlstrom, 1970). Areas of pigment common to larvae of all clupeids from the Gulf include: 1) a row of melanophores above the foregut and below the hindgut, and, 2) pigment above the anus (this study; Houde et al., 1974; Powles, 1977). In addition, Gulf clupeids lack pigment below the foregut. Pigment characters that separate larval clupeid genera include: 1) presence or absence of pigment at the notochord tip and on the nape; and, 2) the SL at which pigment

appears along the cleithrum above and below the axilla of the pectoral fin, dorsally along the hindgut, and along the caudal peduncle (Table 5). Pigment rarely (only once) occurs above the notochord tip in wild-caught preflexion *S. aurita* larvae based on our observations; however, a melanophore was present above the notochord tip in a 7.8 mm laboratory-reared larva illustrated by Houde and Fore (1973, Fig. 3). Most laboratory-reared *B. smithi* (Houde and Swanson, 1975) and wild-caught *B. patronus* (this study) have pigment above and below the notochord tip. Hettler (1984) found one melanophore dorsally and 1–2 ventrally along the notochord tip diagnostic for laboratory-reared *Brevoortia* spp. larvae <8 mm. Most (54%) of our wild-caught *B. patronus* larvae (N = 100) had a single melanophore dorsally, 13% had 2 melanophores, and 33% had no pigment dorsally at the notochord tip. Rarely, neither dorsal nor ventral pigment occurs at the notochord tip. Nape pigment is present either externally or in the musculature of *S. aurita, H. jaguana,* and *B. smithi* larvae at <13–14 mm (Table 5). Pigment does not occur externally on the head or internally on the nape in *O. oglinum* until early transformation (i.e., 15 mm) when internal pigment associated with anterior precaudal vertebrae becomes pronounced (Richards et al., 1974; this study). A pair of external, bilateral melanophores occur dorsal to the hindbrain in *J. lamprotaenia* larvae >9.4 mm but not at the nape until >15 mm (Powles, 1977). *Etrumeus teres* larvae lack nape pigment at <23 mm.

Other characters that separate clupeid larvae include: 1) lack of pigment dorsal to the hindgut, a character diagnostic for larval *O. oglinum* <9 mm; lack of vertical bands of muscle along the hindgut of *J. lamprotaenia* at all sizes (Powles, 1977); and an enlarged hindgut notably thicker than the foregut in preflexion *E. teres* larvae from the Gulf of Mexico (<4.5 mm) and Pacific Ocean (<7 mm, Miller et al., 1979). Preflexion *E. teres* also have a band of melanophores scattered midway along the hindgut that extends onto the ventral finfold, and larvae <20 mm have a gap in pigment dorsally along the anterior third of the hindgut (Miller et al., 1979; this study). This unpigmented gap has been illustrated but not previously discussed (Houde and Fore, 1973; Miller et al., 1979).

Several differences in larval characters occur in *E. teres* literature when compared to our findings. We found 38-39 preanal myomeres in Gulf larvae at <14 mm, and a swim bladder present by 15-16 mm (inflated by 17 mm, although partially obscured by overlying musculature). Larval *E. teres* from along the Atlantic coast of the U.S. have 42 preanal myomeres and lack an air bladder (Fahay 1983). Differences in number of preanal myomeres between *E. teres* from along the U.S. Atlantic and Gulf coasts probably result from differences in how preanal myomeres were counted between studies. The air bladder could have been missed. *Etrumeus teres* from the Pacific Ocean have a swim bladder by 12.6 mm (Miller et al., 1979). In addition, pigment occurs anteriorly on the forebrain of *E. teres* larvae from the Pacific Ocean at all sizes (Miller et al., 1979), but not on the forebrain of Gulf larvae until >23 mm. Finally, Houde and Fore (1973) found pigment along the ventral midline of the caudal peduncle diagnostic for *E. teres* larvae 6–12 mm; however, we found pigment in this area of the caudal peduncle in wild-caught *B. patronus* and *S. aurita* <12 mm, and in *J. lamprotaenia* at all sizes (Table 5).

This paper, because it deals with larvae <15 mm, supplements Houde and Fore's (1973) description of clupeid eggs and their work on larvae >15 mm SL. Houde and Fore's work relies on seasonal occurrence, number of postdorsal-preanal and total myomeres, and fin meristics to identify species, and is particularly valuable for identifying clupeid eggs and also larvae approaching transformation. We believe that early larval pigment patterns must supplement these

characters to identify taxa because of the difficulty and time necessary to count myomeres. Information on larval seasonality is also helpful (Houde and Fore, 1973; Ditty et al., 1988), but must be tempered by the overlap in spawning times and by differences between the northern and southern Gulf for those species spawning Gulf-wide.

In conclusion, the value of counts (e.g., number of postdorsal-preanal and total myomeres) and measurements (e.g., preanal length) lies primarily in separation of taxa into species complexes. Differences in larval pigmentation among taxa, however, will distinguish individual species of clupeids in the northern Gulf of Mexico. The length at which pigment characters first appear should be considered somewhat variable because of differences in growth rate and other factors that can affect larvae when comparing lab-reared and wild-caught specimens. Therefore, separation of individual species should rely on a suite of pigmentation, morphometric, and meristic characters for accurate identification.

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